

Fire Refugia: What Are They, and Why Do They Matter for Global Change?

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Fire refugia are landscape elements that remain unburned or minimally affected by fire, thereby supporting postfire ecosystem function, biodiversity, and resilience to disturbances. Although fire refugia have been studied across continents, scales, and affected taxa, they have not been characterized systematically over space and time, which is crucial for understanding their role in facilitating resilience in the context of global change. We identify four dichotomies that delineate an overarching conceptual framework of fire refugia: unburned versus lower severity, species-specific versus landscape-process characteristics, predictable versus stochastic, and ephemeral versus persistent. We outline the principal concepts underlying the ecological function of fire refugia and describe both the role of fire refugia and uncertainties regarding their persistence under global change. An improved understanding of fire refugia is crucial to conservation given the role that humans play in shaping disturbance regimes across landscapes.

Keywords: biogeography, wildfires, refuge, resilience, landscape ecology

Fire is a global disturbance process that interacts with landscape pattern to create mosaics of ecosystem effects, including patches that remain both unburned and only minimally affected by low-intensity burning. These patches are increasingly of interest to ecologists and are often referred to as fire refugia (Kolden et al. 2012, Robinson et al. 2013, Krawchuk et al. 2016). In the broader ecological literature, refugia are components of ecosystems in which biodiversity can retreat to, persist in, and potentially expand from as environmental conditions change (Keppel et al. 2015). Refugia were originally defined in the context of large-scale processes on evolutionary time scales; continental glaciation and the subsequent isolation of unique habitat types resulted in speciation within refugia (Haffer 1969) and subsequent migrations from refugia (Petit et al. 2003, Brubaker et al. 2005). Refugia created by contemporary ecological phenomena have been the subject of recent studies (Dobrowski 2011, Keppel et al. 2012, Krawchuk et al. 2016, Morelli et al. 2016), reflecting interest in refugia formation and function at smaller spatial and shorter temporal scales, especially in relation to observed and projected climate change. Climate-change refugia have been defined as “areas relatively buffered from contemporary climate change that allow for habitat stability and species persistence over time” (Morelli et al. 2016). However, climate refugia identified for

conservation and management purposes require that these areas also be buffered from severe disturbance events if they are to function as holdouts within a changing environment. Accordingly, fire refugia are a necessary complement to climate change refugia in fire-prone landscapes.

The term *fire refugia* has various definitions (e.g., Gill 1975, Camp et al. 1997, Mackey et al. 2002, Krawchuk et al. 2016), all of which focus on the idea of locations disturbed less frequently or less severely by wildfire relative to the surrounding vegetation matrix. Fire refugia provide habitat for individuals or populations in which they can survive fire, in which they can persist in the postfire environment, and from which they can disperse into the higher-severity burned landscape (Robinson et al. 2013). In this way, fire refugia can function similarly to islands in a biogeographic context, particularly in severely burned areas, recognizing that the matrix of burned areas still provides some habitat to many taxa. Mosaics of fire effects spanning the full range of burn severity—including refugial patches—influence succession, ecosystem processes, and the distribution of biological legacies (Franklin et al. 2000, Turner 2010, Johnstone et al. 2016). Locations in which biota survive fire have been shown to strongly influence postfire recovery and ecosystem dynamics (e.g., Haire and McGarigal 2010, Robinson et al. 2013, Stevens-Rumann et al. 2017). Uniquely, however, fire refugia

are not purely ecological or biophysical phenomena; they are also a socioecological construct—for example, because of human manipulation of vegetative fuels and fire suppression activities that can both facilitate and impede their formation. As patterns of fire refugia are increasingly affected by human activity, understanding their form and function is becoming a priority for conservation, management, and policy. Recognition and identification of fire refugia, including their spatial configuration, their physical location within the surrounding burned matrix, and their composition and structure will become increasingly important for effective conservation and land management under the nexus of altered land use, shifting land cover, and anthropogenic climate change, which we hereafter refer to as *global change*.

Given the growing interest in and number of publications on the form, function, and conservation value of contemporary fire refugia (Kolden et al. 2015a), our objective is to synthesize the existing literature and characterize the current thinking about fire refugia in forested ecosystems in the context of global change. By defining and identifying different aspects of fire refugia, we provide a clearer architecture for these important landscape elements, as a crucial step forward in refugia-based science and management. We address three overarching questions: First, what are fire refugia? That is, what are the commonalities and differences in the ways fire refugia have been defined in the scientific literature? Second, what theoretical frameworks underlie the ecological function of fire refugia? Third, how can fire refugia support ecosystem resilience under global change? We expand considerably on prior efforts by Robinson and colleagues (2013) by including flora and by focusing on refugia as microecosystems rather than as habitat only for a specific faunal species of interest. In addition, we characterize the temporal dynamism of refugia by addressing drivers of formation and persistence. Finally, we address global change and the role of refugia in ecosystem resilience. By clearly defining and identifying different aspects of fire refugia, we gain insight into whether they will persist or whether there are given thresholds that might lead to losses in fire refugia in a time of accelerating global change. To support our synthesis, we conducted a comprehensive literature search using standard scientific search engines (e.g., Web of Science, Academic Search Premier) and searched for all known terms used for fire refugia (e.g., *skips*, *unburned islands*, *refuges*) in sources published as of June of 2018. We then compiled these to identify common themes and determine which key research best highlighted the facets of these common themes (supplemental tables S1 and S2). We acknowledge that some studies that fall within broader definitions of fire refugia and more tangential research may be omitted from these tables.

What are fire refugia?

Fire refugia are defined and characterized variably in the literature. Other terms used to describe them include *unburned islands*, *habitat refugia*, *remnants*, *residual vegetation*, *fire shadows*, *skips*, *stringers*, *refuges*, *islands*, *biological legacies*,

and *late-successional forest* (tables S1 and S2). Studies of fire refugia have been concentrated primarily in the boreal and temperate forests of western North America and the shrublands and forests of eastern Australia, with additional studies in Europe, South America, and Africa (tables S1 and S2). There is some ambiguity in the literature regarding the distinction between *refugia* and *refuges*, which we suggest is more of a language clarification than a formally defined difference. Although there are reasons to consider refugia and refuges differently, we recognize that both are focused on the same core idea—areas that are buffered from pressures or changes experienced by adjacent areas. From Camp and colleagues (1997), one of the early seminal works on fire refugia, and to be consistent with the authors' more recent contributions in this field, we use *refugia* in the present article rather than *refuges*. On the basis of the existing literature, we identify four taxonomic dichotomies that delineate a conceptual framework for characterizing fire refugia: unburned versus lower severity, species-specific versus landscape-process characteristics, predictable versus stochastic formation, and ephemeral versus persistent. We describe each of these in a global change context.

Unburned versus lower severity refugia In some studies, fire refugia are defined specifically as unburned areas within fire perimeters (Meddens et al. 2016, Swan et al. 2016), whereas in others, the definitions include low-severity fire patches within the burned area (Krawchuk et al. 2016). Many researchers, however, do not explicitly define whether fire refugia are unburned, low severity, or a mixture of the two (e.g., Camp et al. 1997, Schwillk and Keeley 2006). The widespread use of Landsat-based change detection methods to generate maps of burn severity and identify fire refugia has led some researchers to describe relatively large areas as unburned (Roman-Cuesta et al. 2009, Wood et al. 2011, Kolden et al. 2012, Kolden et al. 2015a, Meddens et al. 2016) but has also yielded a growing recognition that it is difficult in some ecosystems to accurately differentiate between unburned islands and low-severity patches from such spectral reflectance-based remote-sensing data sets (van Wageningen and Lutz 2007, Kolden et al. 2015b). This difficulty stems from the variability of subcanopy surface conditions within a pixel when the imagery values primarily reflect conditions associated with an unaffected overstory canopy (Cansler and McKenzie 2014). Furthermore, the delineation of refugia from spectral data without additional ground observations does not provide information on the prefire composition and structure of the fire refugia (Meigs and Krawchuk 2018) or their potential ecological functions.

A definition of fire refugia that includes areas that experienced underburns, surface fire, or low fire severity, in addition to areas that were truly unburned, reflects a broader and more inclusive perspective of refugia that supports the preponderance of taxa and fire effects of interest for conservation and management concerns. For example, in a forested ecosystem, a stand of trees in which the surface has

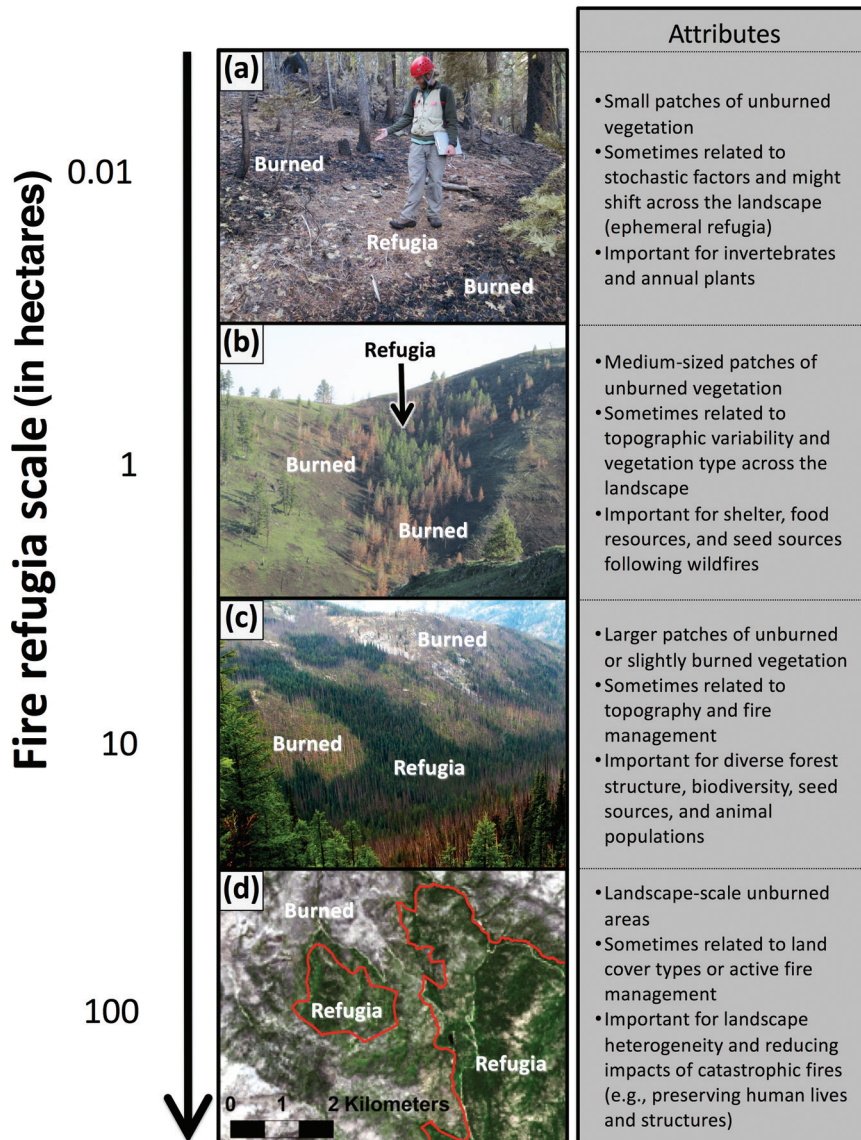


Figure 1. Examples of different spatial scales of fire refugia: (a) small patch of unburned forest floor from the Rim Fire in California (2013), (b) unburned overstory ponderosa pine (*Pinus ponderosa*) stand from the Big Cougar Fire in Idaho (2014), (c) larger unburned island within forested areas from the Butte Creek fire in Washington (1994), and (d) natural color Landsat scene subset from the Carlton Complex fire in Washington (2014).

moved through the understory, leaving the canopy intact when the surrounding area burned at a high severity would be considered a fire refugium. The overstory trees in this fire refugium were resistant to fire, persisted as legacies on the landscape, and will function as seed source for forest reestablishment. Surface fire in fire refugia may, in fact, increase the chances of the overstory community persisting through subsequent events—for example, as “fire-tended” old growth forest fire refugia. In comparison, a nearby stand may have received no fire, and this unburned area is also a fire refugium but with different compositional and structural attributes. Researchers and managers interested

in specific ecosystem components, such as rare, fire-intolerant species, understory vegetation, surface fuels, or below-ground processes would likely define refugia more restrictively (tables S1 and S2). The inclusive definition of fire refugia, with recognition of the distinctions between unburned and low-severity fire refugia, is crucial in integrating the role of refugia across broad regions and fire ecologies.

Species-specific refugia versus landscape process Studies of fire refugia generally fall into two broad research perspectives (Lindenmayer 2009): fire refugia specific to a species or group of species (table S1) and fire refugia as the product of landscape-scale processes (table S2).

A species-oriented perspective is focused on how taxa (or their habitat) respond to direct exposure to combustion and fire-induced habitat change; this perspective is covered in depth by Robinson and colleagues (2013). Existing species-oriented fire refugia research includes studies of butterfly populations, invertebrates, bryophytes, birds, small mammals, and vegetation (table S1). These studies stem from the need to understand specific mechanisms of survival, connectivity, dispersal, and the persistence of species and populations during and after wildfires, particularly when a species is threatened or endangered. Species-specific refugia can refer to single plants (requiring refugia of only a few square meters) that remain unburned and shelter invertebrates (e.g., Brennan et al. 2011) or larger areas (tens to hundreds of square meters) that remain unburned and promote persistence

of plant species and vertebrates that rely on these structural elements as habitat (e.g., Banks et al. 2012; figure 1). Species-specific refugia may also involve larger unburned or lightly burned patches or collections of patches that maintain a single species across the larger landscape (e.g., *Pinus sabinana* in Schwillk and Keeley 2006). To meet regulatory mandates to preserve such species under global change, however, habitat requirements must be embedded in more comprehensive landscape processes that facilitate specific ecosystem functions, particularly when multiple management objectives must be met.

Landscape-process fire refugia have primarily been characterized as landscape patches that did not burn or that burned less severely or frequently than adjacent areas did, irrespective of species composition (cf. Berry et al. 2015b). In contrast to a species-specific approach, research focused on landscape-process refugia is generally intended to quantify and characterize patterns of fire refugia across a range of spatiotemporal scales and to associate refugial formation with environmental factors (Lindenmayer 2009; table S2, figure 1). This approach is often embedded within broader landscape ecology theory or remote-sensing queries and analyses (e.g., Kolden et al. 2012, Kane et al. 2015, Meigs and Krawchuk 2018), but landscape-process studies also include modeling (Wimberly and Kennedy 2008) or quantification of forest stand structure and composition from field observations (Camp et al. 1997). In contrast to species-centric perspectives, landscape-process studies often lack quantifiable mechanistic links to the fine-scale ecological processes that are important for understanding ecological function of fire refugia. However, landscape-process studies (table S2) can inform efforts focused on ecosystem process, particularly those interested in trends and patterns of reforestation and plant regeneration under global change (e.g., Stevens et al. 2017). Similarly, landscape-process studies may inform species-specific management objectives by identifying changes in patch metrics of crucial habitat, such as the optimal patch-size distributions of shade for ectotherms (e.g., Sears et al. 2016).

Predictable versus stochastic refugia formation For any given fire event, fire refugia are formed through fire behavior driven by the three factors of the fire behavior triangle: topography, fuels, and weather. These three factors control fireline intensity and direction of spread. A change in any factor can deprive a fire of available fuel, creating refugia. Water features, riparian areas, roads, and clearings are some of the most obvious contributors to stopping or slowing fire spread, thereby providing a degree of predictability to the occurrence of fire refugia in the vicinity. Topography and edaphic factors, including surface soil characteristics, are enduring features that are more stable than fuels or weather, and they influence the predictability of where fire refugia occur (Camp et al. 1997, Perera and Buse 2014, Krawchuk et al. 2016). Specifically, permanent topoedaphic features, such as rock outcrops, ridges, or scree slopes, can function as firebreaks that protect adjacent vegetated areas, because they are unburnable, and they may also serve as refugia for species that can inhabit these environments. At the same time, fire refugia are more likely to occur in valley bottoms, local concavities, draws, or gullies (Bradstock et al. 2010, Leonard et al. 2014, Krawchuk et al. 2016), potentially as a function of cold air pooling (Wilkin et al. 2016), and through increased soil and fuel moisture (Romme and Knight 1981, Coop and Givnish 2007). Slope, aspect, and elevation also can play a role, such that cooler and moister sites burn less frequently and support late-successional, fire-resistant individuals and

populations (Camp et al. 1997, Wood et al. 2011). Under more extreme dry and hot weather conditions, however, these facets may lose their protective characteristics and burn more severely because of high fuel accumulation (Beatty and Taylor 2001, Krawchuk et al. 2016).

By contrast, fire refugia formation can also be driven by stochastic factors. Sudden wind shifts, fire-generated behavior (e.g., fire whirls and self-generating weather), and changes in weather are all frequent causes of fire refugia formation as an advancing flaming front skips over an area. This is particularly characteristic of fire refugia formed in discontinuous fuels or landscapes with benign terrain (Krawchuk et al. 2016), in which fire spread depends strongly on wind, and therefore, fire refugia formation is similarly related to wind patterns. Importantly, human actions related to fuel management and fire suppression can be more challenging to predict consistently. People build fire breaks and containment lines around resources at risk, intentionally making those resource areas into fire refugia. At the same time, humans unintentionally create refugia through activities that alter fuel continuity (e.g., off-highway vehicle trails, resource extraction activities such as logging or drilling, and clearing of surface fuels through firewood gathering), facilitating changes in fire behavior. Part of the current challenge in distinguishing predictable from stochastic refugia formation is that much of the science currently depends on imperfect post hoc reconstruction of fire events, with the most predictable refugia being those that have persisted through multiple wildfires.

Ephemeral versus persistent fire refugia Over multiple fire-return intervals, fire refugia that last through only a single fire event are defined in the present article as *ephemeral*, whereas refugia that survive through multiple fires are defined as *persistent* refugia. Generally, persistent refugia are formed through relatively predictable processes, and ephemeral refugia are formed through stochastic factors, but this is not always the case. For example, some ephemeral refugia may be predictable if they remain unburned under more benign or moderate conditions (e.g., a meadow above a certain threshold of soil moisture) but may burn at other times (e.g., the same meadow in an extreme drought year); such refugia would be predictable, because the conditions prescribing their formation are known, but they would not necessarily persist through multiple fires (Perera and Buse 2014, Berry et al. 2015a, Krawchuk et al. 2016). Although ephemeral refugia remain only through individual fire events, the aggregate population of these refugia over landscapes and regions may be important in supporting the persistence of refugia-associated species over longer timeframes and under global change.

By contrast, persistent fire refugia are those that remained intact through multiple fire events (including reburns; Prichard et al. 2017), and this persistence suggests that they are more likely to be predictably associated with stable

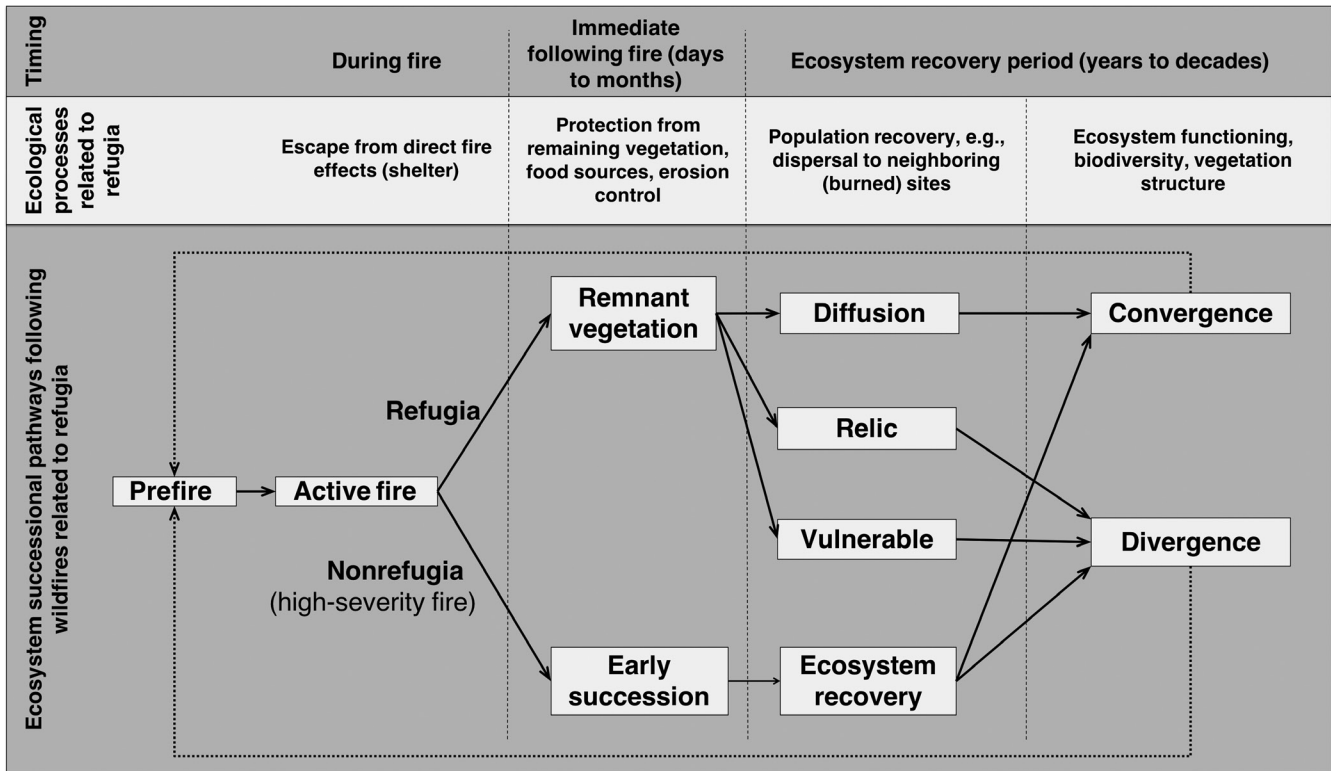


Figure 2. Successional pathways of refugia and nonrefugia following fires in relation to the broader ecosystem. During and immediately after fire, refugia provide shelter or food resources, whereas over longer time periods fire refugia facilitate ecosystem recovery by providing seed sources and increasing biodiversity. The burned area can recover to similar vegetation as the preburn condition, leading to convergence of refugia and the surrounding matrix maintaining prefire ecosystem function. However, if the surrounding matrix transitions to a different ecological state, the refugia become a relic or are left vulnerable to subsequent disturbance, leading to a divergence from prefire ecosystem function.

landscape features (Clarke 2002). Fire-resistant conditions may also occur through self-reinforcing fire-vegetation feedback loops that are either natural (e.g., Wood et al. 2011) or human induced through repeated intentional burning, such as annual indigenous burning to protect key resources (Kimmerer and Lake 2001). Ephemeral and persistent fire refugia can provide similar ecological functions (e.g., as seed sources; Weisberg et al. 2008). However, persistent refugia are more likely to provide unique structures and functions associated with late-successional ecosystems (e.g., diverse structural conditions; Camp et al. 1997, Kolden et al. 2015a), older individuals (e.g., large-diameter trees; Lutz et al. 2013, Lutz et al. 2018), or landscape context (e.g., position or configuration; Russell-Smith and Bowman 1992). Persistent fire refugia may also be more vulnerable to losses associated with anthropogenic climate change and changing fire regimes (Kolden et al. 2017), because the climatic conditions that previously sustained persistent refugia may give way to conditions that support and facilitate fire spread into a previously persistent patch. This novel introduction or reintroduction of fire would have considerable implications for ecosystems that have been dependent on such refugia.

The ecological functions of fire refugia

The ecological functions of fire refugia depend on the reproductive age, mobility, and fire sensitivity of the biota within them; the contrast between refugia and the surrounding burned matrix; and the postfire successional trajectories of nearby burned areas. The differential ecological functions of fire refugia also change over time after a fire (Robinson et al. 2013, Perera and Buse 2014). For instance, refugia can shelter and protect fauna during an active wildfire, function as remnant habitat immediately postfire, or support population reestablishment in the years to decades following fire (figure 2). In this way, refugia variably function as islands in a biogeographic context or as patches in a landscape matrix.

During the fire Areas within the fire perimeter that provide shelter or protection from fire effects are key to maintaining populations and seed sources. Biota with limited or no mobility and limited resistance to fire effects (e.g., butterflies, snails, annual plants, and fire-intolerant woody plants) will be locally extirpated from the ecosystem without shelter from combustion and radiant heat (Hylander and Johnson 2010, Hylander 2011). Refugia generally comprise these unburned areas or

slightly burned areas in which fire energy does not reach a lethal dose (Hylander and Johnson 2010, Gongalsky et al. 2012, Smith et al. 2017). More mobile taxa, such as ungulates and birds, may use refugia to evade flames (Henriques et al. 2000, Lindenmayer et al. 2009, Banks et al. 2011), but they could be more vulnerable to the immediate and longer-term postfire effects on the landscape (Banks et al. 2012).

Immediate postfire Remnant vegetation following fire provides functional habitat and other crucial ecological functions days to months after fire. Refugia can supply food resources (Schwilk and Keeley 1998, Henriques et al. 2000) that are otherwise consumed by fire in the surrounding landscape, provide cover or protection from predators, or reduce influences from exposure to abiotic stressors (e.g., wind and solar radiation). Competition within refugia may increase from before to after a fire, because of decreases in available resources in the surrounding burned landscape (Banks et al. 2012). In addition, these refugia can function as buffers against erosion and landslides that can occur following fires (Shakesby and Doerr 2006), mediating detrimental habitat loss.

Recovery period Depending on the severity of the surrounding burned area, refugia can function as biogeographic islands during the early recovery period. They increase habitat variability on the landscape, providing patches with later successional species interspersed within an early successional landscape (e.g., Swanson et al. 2010), thereby increasing beta diversity within a given fire perimeter. Fire refugia also can function as long-term, postfire habitat from which species can expand to neighboring areas, effectively functioning as a seed source (e.g., diffusion; figure 2; Schwilk and Keeley 2006, Stevens-Rumann et al. 2017). Environmental conditions (e.g., climate) and the recovery trajectory of the surrounding vegetation determine whether refugia merge with recovering vegetation and ultimately maintain prefire ecosystem function (convergence), or the surrounding vegetation recovers differently from how fire refugia do, resulting in a change of ecosystem function (e.g., divergence; figure 2). Relic refugia may persist in the postfire landscape, but if the structure or composition of surrounding vegetation transitions to a new state, refugia may no longer support prefire ecosystem function; Lindenmayer and colleagues (2011) described these as *landscape traps*. For example, anthropogenic climate change may be facilitating type conversion of forest to shrublands in some regions by inhibiting seedling regeneration (Stevens-Rumann et al. 2017), and relic forest refugia unable to regenerate the forest around them may be vulnerable to further disturbances, such as cases in which a new surrounding vegetation matrix has a higher vegetative fuel load or shorter fire return interval than the prior matrix (figure 2; Kolden et al. 2017), potentially leading to total loss of forest habitat for that site.

Fire refugia and global change

Climate change has increased both fire potential and realized fire activity in many parts of the world (Jolly et al. 2015, Abatzoglou and Williams 2016). The greatest recent increases have been observed in boreal forests and tundra (Andela et al. 2017), consistent with observations of the most rapid rates of climate change in high latitudes (IPCC 2013). In the western United States, increased fire extent in recent decades (Westerling 2016) has been attributed to myriad factors, including past fire suppression, land use and land cover changes, and increased ignitions by humans (Balch et al. 2017), as well as anthropogenic climate change (Abatzoglou and Williams 2016). Climate change is projected to continue to increase the potential for large, destructive fires across the United States (Barbero et al. 2015) and globally (Bowman et al. 2017), albeit with heterogeneous impacts to realized fire activity across the broader region (Kitzberger et al. 2017).

This considerable increase in fire has prompted questions of whether fires are also increasing in severity and completeness of combustion, which should hypothetically reduce the occurrence and extent of fire refugia. To date, there is mixed evidence that fires are burning more severely over the contemporary record, outside of a few isolated subregions (e.g., Picotte et al. 2016, Abatzoglou et al. 2017), and climatic conditions do not appear to be a strong driver of burn severity (Birch et al. 2015, Abatzoglou et al. 2017). Some studies focused on high-severity fire have shown increases in high-severity patch interior (Cansler and McKenzie 2014, Stevens et al. 2017), implying that small scale refugia—such as individual trees that serve as a seed source—may be becoming rarer in some landscapes, but higher-resolution data are needed to confirm the loss of these small-scale refugia. Studies focused solely on fire refugia have shown no trends toward reduced or altered patterns of refugia, suggesting that fires are burning neither more completely nor more severely (Kolden et al. 2012, Kolden et al. 2015a, Meddens et al. 2018). Nor are there clear or strong relationships between climate and patterns and proportions of fire refugia across regions (Kolden et al. 2012, Kolden et al. 2015a, Meddens et al. 2018). Instead, local-level topography seems to be a strong driver of refugia patterns, although importantly, the capacity for terrain features to support refugia appears to diminish under more extreme daily fire weather conditions (Roman-Cuesta et al. 2009, Krawchuk et al. 2016).

The fire refugia studies described in the preceding paragraph defined fire refugia on the basis of landscape process rather than the species-specific definition, so it is unknown whether these trends are applicable to refugia for specific species of interest. Species-specific or biodiversity-focused approaches for fire refugia may show global change trends that are not evident when a landscape-process approach is used. For example, in the boreal forest of North America, climate change and increased fire activity are already thought to be facilitating the loss of continuous permafrost that is required for the regeneration of black spruce (*Picea*

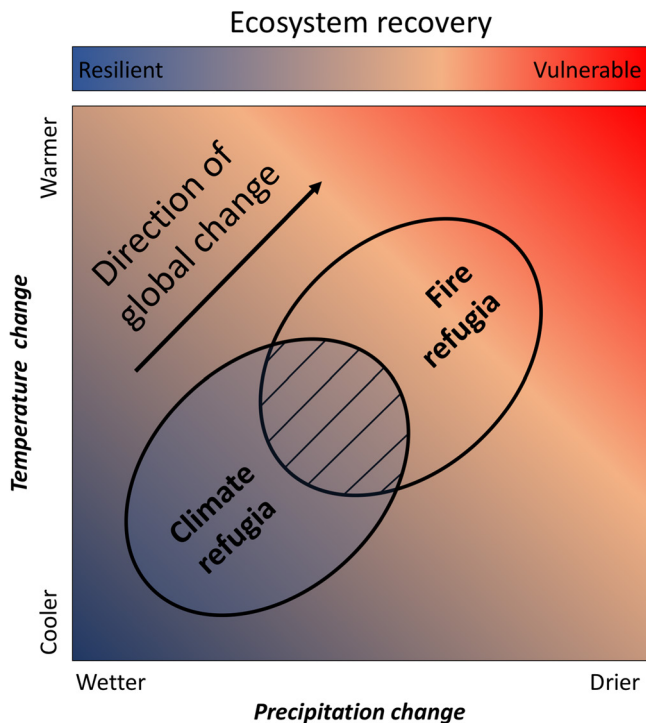


Figure 3. Conceptual effect of global change on ecosystem recovery in relation to climate and fire refugia, adapted from Allen and colleagues (2010). The ovals indicate the fire refugia and climate refugia that exist under current and persist under future conditions. Because of topographic connections to both fire and climate refugia, there is likely a partial overlap between the two refugia types (hatched area) across the landscape. Climatic impacts on fire refugia are expected to shift more rapidly as opposed to climate refugia, because climate refugia are more buffered from these global changes. Identifying the geospatial overlap between fire refugia and climate refugia is an important research need.

mariana). This ecosystem is transitioning to white spruce- and deciduous-dominated conditions, leaving fire refugia vulnerable to extirpation by subsequent fire (Johnstone et al. 2016). Similarly, the invasive spread of exotic annual grasses into the arid and semiarid regions of North America and Australia has induced more frequent fire, facilitating a type conversion to annual grassland. Shrub-steppe fire refugia that serve as crucial habitat for species of concern are vulnerable to loss in subsequent fire, completing the type conversion by removing the regeneration seed source (D'Antonio and Vitousek 1992, Rossiter et al. 2003).

Although changing fire regimes may influence the distribution and quantity of fire refugia, fire is a naturally occurring, dynamic agent of ecosystem change in most seasonally dry ecoregions. As anthropogenic changes continue to alter ecosystems, there is renewed focus on refugia as key components of ecosystem resilience that will buffer some of the more immediate negative impacts of climate change (Keppel

and Wardell-Johnson 2012, Taylor et al. 2014). For example, climate and land use changes increase the vulnerability of ecosystem services (Smith et al. 2014), whereas fire refugia can mitigate the negative effects of altered disturbance regimes by providing places in which species that are not adapted to new disturbance regimes can persist, migrate through, or adapt in place (Dobrowski 2011). In addition, plant seedling establishment and persistence are related to the availability of seed sources but also to climatic conditions. Juveniles tend to occupy a cooler and wetter niche (Dobrowski et al. 2015), so refugia such as old-growth forest that foster locally moderated microclimate conditions by providing shade (Frey et al. 2016, Lutz et al. 2018) may improve their establishment success on adjacent sites, particularly as increased summer drought may negatively affect ecosystem recovery (Harvey et al. 2016, Stevens-Rumann et al. 2017).

Given projections of warmer and sometimes drier conditions in the future, colocation of fire refugia and climate refugia will become more important for effective function of fire refugia (Wilkin et al. 2016). When these refugia are not colocated, ecosystem recovery potential might be severely hampered, because recovering species are pushed out of their historic climatic envelope (figure 3). Therefore, the spatial arrangement of fire refugia may play a key role in how landscape heterogeneity buffers ecosystems from anthropogenic climate change. This buffering role is especially important where colocated refugia support or facilitate recovery of the predisturbance ecosystem function, whereas fire refugia that do not overlap with climate refugia are more vulnerable to being compromised (figure 3). For example, because drought refugia are more resistant to the extremes of interannual climatic variability, it is hypothesized that such locations will continue to be buffered as the climate changes (McLaughlin et al. 2017), thereby harboring remnant populations of sensitive species prioritized by conservation adaptation and mitigation solutions (Morelli et al. 2016). However, this hypothesis depends on climate feedback loops not reducing the resilience of refugia through increased ecological disturbances, such as wildfire, bark beetles, and drought.

Research needs and management implications

There is a crucial need to prioritize fire refugia for conservation and management under global change. The fire refugia taxonomic dichotomies presented in the present article provide a framework to consider conservation values and potential trends in fire refugia characteristics. Understanding the distribution, abundance, composition, and function of fire refugia may help in prioritizing land management activities on the basis of the concepts of resistance and resilience to fire and of the vulnerability to further disturbances. This prioritization will likely require a comprehensive understanding of both the spatial and the temporal predictors of refugia, integrated with conservation needs and policy limitations.

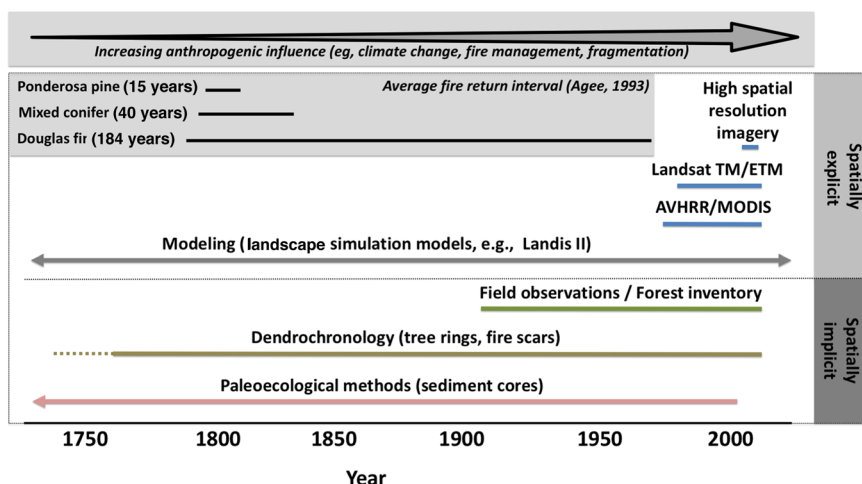


Figure 4. Examples of approximate timescales at which different methods or instruments can contribute to understanding of wildland fire and the occurrence of fire refugia. Average fire return intervals for three different ecosystems across the western United States are given with the bars representing the time period across the time axis.

Because the patterns of fire refugia can be affected by human activity and because the management of fire refugia has considerable implications for conservation and policy, there is a need for research integrating different spatial and temporal methodologies to improve understanding of the ecological function of fire refugia (figure 4, table 1). Integration of field and remote-sensing data into both statistical and simulation modeling frameworks has been proposed to facilitate dynamic species distribution modeling under global change (Franklin et al. 2016), and such integration also holds great potential to enhance the understanding of fire refugia by scaling across space and time (e.g., O'Connor et al. 2016). For example, consider a study identifying the minimum areal extent and canopy cover for refugia required by a specific species as habitat in the field. This estimate could then be extended geospatially by predicting the number of refugia that meet the criteria from remote sensing and modeled into the future from downscaled global climate model outputs and landscape-scale ecosystem simulations. Linking species-specific and landscape-process approaches could also help identify criteria for land managers wishing to conserve species and habitats in fire-prone landscapes. The challenge is that such approaches require large calibration areas to link across scales (Lutz 2015).

Because fire activity is projected to increase under future climate scenarios, fire refugia will likely be important to preserving ecosystem resiliency for a variety of taxa (tables S1 and S2). Therefore, future management actions should focus on identifying, maintaining, or promoting fire refugia within landscapes holistically. For example, the actual locations of ephemeral fire refugia may be less important than their aggregate area and their spatial configuration. On the other hand, understanding the location and environmental

determinants of predictable, persistent, and semipersistent fire refugia may be vital for increasing the resilience of both natural and human-occupied landscapes (Smith et al. 2016).

Management actions specifically designed to support the formation and conservation of fire refugia generally do not yet exist or have not been tested for efficacy. However, one management strategy that would have clear positive outcomes for conserving fire refugia could be reducing the use of backfires and burnouts (or “blackout burning”) as wildfire suppression tactics where feasible. During large fire events, firefighters routinely use firing operations to consume available fuel ahead of an advancing fire front; as the flaming front passes or reaches containment lines, they subsequently burn out any remnant green vegetation (i.e., fire refugia) to reduce

the potential for flare-ups and ember-ignited spot fires across the containment line. Although this operation tactic is highly effective for protecting crucial infrastructure and resources, it may not be necessary to achieve containment on fires that are remote or being managed to meet natural resource objectives. One strategy for addressing the potential loss of fire refugia from this practice is to embed fire refugia in national and global conservation plans through entities such as The Nature Conservancy and Conservation International, which work with regional and local partners to identify the best management practices and policies to support ecological conservation.

Targeted suppression efforts can be used strategically to protect sensitive refugia. For example, giant sequoia (*Sequoiadendron giganteum*) groves that historically burned at low severity prior to modern fire suppression have specifically been protected through preventative prescribed fire, silvicultural treatment, and subsequent enhanced suppression efforts in several recent fires in Yosemite and Sequoia and Kings Canyon National Parks in California. To date, fire refugia are generally not considered “at risk,” or areas worth protecting during fire suppression activities. Identifying ecologically valuable fire refugia or locations on the landscape in which significant proportions of fire refugia are desired in the postfire mosaic would allow fire managers to integrate the conservation or formation of fire refugia into their pre-planning, strategy and tactics (e.g., Dunn et al. 2017).

Conclusions

Fire refugia are crucial for the maintenance of biodiversity and ecosystem resilience under global change (Keppel and Wardell-Johnson 2012) but may also be at risk because of feedback loops of a changing climate, land management, and fire management practices. Projected increases in fire

Table 1. Future key research needs and their associated management and applications questions for fire refugia.

Topic	Key research need	Key management and applications questions
Historic natural variability	Historical range of refugia abundance, size, and complexity across ecotypes ^{a,b,c,d,e,f}	How do we facilitate refugia through ecosystem restoration tactics (e.g., prescribed fire)?
Refugia characteristics	Ranked importance of refugia characteristics by key species ^{b,e}	How do we integrate metrics of refugia (e.g., distribution, abundance, physical complexity) into ecosystem function management goals?
Landscape pattern	Refugial connectivity across landscapes; species-specific needs for network size and connectivity ^{e,g,h,i,j,k,l,m,n,o,p,q}	How do we create refugial connectivity on the landscape through forest and fire management activities?
Biophysical determinants	Relationships between refugia longevity and biophysical factors (persistent, predictable, stochastic) ^{e,f,r,s,t,u,v,w}	How and where can we establish biophysical barriers to create, enhance, or preserve fire refugia on the landscape?
Fire behavior	Models of fire behavior that accurately project refugial formation ^{d,e,x}	Under what conditions can we actively pursue protection or facilitation of fire refugia?
Climate change	Climate change impacts on refugial trajectories, patterns, function, and characteristics ^{y,z}	How do we identify and protect crucial fire refugia as seed sources and biodiversity hot spots?
Successional pathways	Probabilities of different successional pathways for refugia ^{e,w,aa,bb,cc}	How do we protect the ecological integrity of fire refugia years to decades after a fire?

Note: Literature that in some way or form contributes to or highlights the need for (a) research, (b) management, or (c) applications, related to fire refugia: ^aMeddens et al. 2016, ^bMeddens et al. 2018, ^cKolden et al. 2012, ^dKrawchuk et al. 2016, ^ePerera and Buse 2014, ^fRobinson et al. 2013, ^gBanks et al. 2012, ^hBanks et al. 2011, ⁱBerry et al. 2015b, ^jBrennan et al. 2011, ^kGongalsky et al. 2012, ^lHenriques et al. 2000, ^mHylander 2011, ⁿHylander and Johnson 2010, ^oLindenmayer et al. 2009, ^pSchwilk and Keeley 1998, ^qSwan et al. 2016, ^rBerry et al. 2015a, ^sClarke 2002, ^tLeonard et al. 2014, ^uRoman-Cuesta et al. 2009, ^vWilkin et al. 2016, ^wSchwilk and Keeley 2006, ^xWimberly and Kennedy 2008, ^yAbatzoglou et al. 2017, ^zKolden et al. 2015a, ^{aa}Camp et al. 1997, ^{bb}Harvey et al. 2016, ^{cc}Kolden et al. 2017.

season duration and fuel aridity in response to anthropogenic climate change alongside invasion of exotic annual grasses are expected to increase future fire activity across both moist and arid ecosystems, which, in turn, will increase the importance of fire refugia. The ecological functions of refugia—locations in which biodiversity can retreat to during and immediately after fire, and persist in and expand from following fire—will continue to be important for overall ecosystem resilience. The four dichotomies in our fire refugia taxonomy clarify the full spectrum of fire refugia characteristics while facilitating their identification and classification. This holistic approach to thinking about fire refugia, which includes both landscape-process and species-specific perspectives, can help contextualize future research that investigates the formation, function, or conservation of fire refugia, and can also be incorporated by land managers into fire management strategies from local to global scales.

Supplemental material

Supplemental data are available at *BIOSCI* online.

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Fire refugia: What are they and why do they matter for global change?

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Supplementary material

Contents:

Table S1. Summary of reviewed studies involving species-specific wildfire refugia.

Table S2. Summary of reviewed studies involving landscape-scale wildfire refugia.

WebTable 1. Summary of reviewed studies involving species-specific wildfire refugia.

Study	Objective of study	Species of interest	Location	Extent / spatial domain of study	Ecosystem type	Fire refugia definition or characteristics	Refugia age	Refugia size	Main conclusions	Sever-ity ^a	Predic-tability ^b	Persis-tence ^c
Schwilk and Keeley 1998	Evaluate relationship between rodent populations and distance to unburned brush	Rodents (Eight different species)	Big Sycamore Canyon, Point Muga State Park, California, USA	A 110 m transect with traps every 5 m, at six sites ranging in elevation from 75 m to 210 m within the canyon	Coastal sage scrub and chaparral	Unburned vegetation outside fire perimeter (chaparral or coastal sage)	N/A	N/A	Rodent response to distance to unburned areas differed by species, and by habitat type (coastal sage scrub vs. chaparral)	U	N/A	N/A
Pfab and Witkowski 1999	Determine whether an endangered succulent survives fire in refugia or via fire tolerance	A succulent species (<i>Euphorbia clivicola</i>)	Northern Province of South Africa	An unknown number of transects 5 m apart	Savannah, grassland	Rocky patches with lower fuel amounts	N/A	N/A	Fire refugia were not associated with survivorship of the plant species studied. In contrast, plant seems to be fire tolerant and a resprouter that regenerates following low severity fire	U/L	P	P
Henriques et al. 2000	Describe the changes in small mammal populations in a patch of unburned woodland	Seven species of small mammals (6 rodents and 1 marsupial)	Southwest Brasília, Brazil	Two sampling grids with 49 stations 10 m apart (one in the unburned areas and one in the burned area)	Semi-deciduous cerrado woodland	One unburned patch of 1 ha	Measured 6 months after the fire	1 ha	Data suggest that many species use the unburned cerrado patch as shelter during the fire and/or as a food sources after the fire	U	S	E
Swengel and Swengel 2007	Determine the spatial and temporal patterns of fire refugia in association with butterfly abundance	Butterfly species (Lepidoptera species)	Three sites in Wisconsin, USA	Crex Meadows: 12,180 ha Bauer-Brockway: 125 ha Muralt Bluff: 25 ha	Pine barren, prairie fields, oak savanna	Unburned units compared to surrounding sites with more frequent fire	>6-8 years	Ave: 7 ha (range: 3-14ha)	Areas started functioning as refugia for butterflies 6-8 years after burning	U	N/A	E
Gandhi et al. 2001	Determine whether fire residuals are important for beetles and whether patch size is correlated with beetle population diversity	Litter-dwelling beetles (Coleoptera: <i>Carabidae</i> and <i>Staphylinidae</i>)	Western Alberta, Canada	Sixteen refugial patches across two wildfires that burned 1,015 ha	Montane and boreal forest	Fire residuals were wet, late successional patches of fir and spruce stands	Average 180 years, oldest trees were 300 years	Ave: 1.5 ha (range: 0.012 – 10.8 ha)	1) Trees in residual significantly older than surrounding; 2) greater diversity in residuals compared to burned areas; 3) no relationship between residual size and species diversity	N/A	N/A	N/A
Brotons et al. 2005	Determine importance of dispersal on avian post-fire colonization	Nine open-habitat bird species	Catalonia, Northeastern Iberian Peninsula, Spain	Transects on 8 wildfires (273–5,905 ha), which were at least 10 km from each another	Mediterranean forest (pine, cork-oak, or holm-oak) and shrubland, including grasslands and rocky outcrops	N/A	N/A	N/A	Strong significant differences in post-fire species composition between burnt areas, indicating the importance of landscape heterogeneity (including unburned areas) resulting from wildfires	N/A	N/A	N/A
Schwilk and Keeley 2006	Test hypothesis whether gray pines spread from unburned areas to upland chaparral ecotones in the region	Gray pines, <i>Pinus sabiniana</i>	McNally fire, California, USA	Seven (50×500 m) transects in a 25,100-ha fire	Gray pine and chaparral	Gray pine populations persist in reduced fire severity riparian areas	N/A	Average widths of riparian valleys: 79-177 m	Maximum age of gray pines declined significantly with distance to riparian areas, suggesting the need for fire refuges for reinvasion of slopes after being eliminated by severe fires	L	P	P

Lindenmayer et al. 2009	Quantify post-fire recovery of the Eastern Bristlebird	Eastern Bristlebird (<i>Dasyornis brachypterus</i>)	Booderee National Park, southeastern Australia	Bird occurrence was recorded at 110 sites a year before and for 3 years after a fire	Different vegetation types including heathland, woodland, shrubland, forest and rainforest	Field surveys indicating unburned sites	Measured up to 3 years post-fire	N/A	Rapid bird population recovery of burned sites was most likely due to movement by resident birds to unburned parts elsewhere within their territories	U	N/A	N/A
Hylander and Johnson 2010	Do unburned areas support higher diversity and abundance of bryophytes?	Boreal forest bryophytes	Tyresta National Park, Sweden	Fourteen burned and 12 forest reference plots (50 by 50 m) within each plot 15 random 1-m ² micro-plots	Boreal forest (pine, spruce, broadleaf)	Refugia generally related to rocky or mesic conditions rather than wet conditions	Measured 7-8 years post fire	Not stated but generally on the scale of m ²	(1) Refugia were associated with rocky sites (fuel breaks) rather than wet sites (2) Refugia within the fire perimeter were more like the surrounding unburned forest than the burned forest (3) Colonization from refugia unclear	U	N/A	N/A
Banks et al. 2011	Quantify the effects of high severity forest fire on the population characteristics of mammal species	Two small mammal species (<i>Antechinus agilis</i> and <i>Rattus fuscipes</i>)	Black Saturday fires, Victoria, Australia	Fifteen trapping sites, dispersed over the fire (including unburned areas)	Tall eucalypt forest (dominated by <i>Eucalyptus regnans</i>)	Unburned sites outside fire perimeter	N/A	N/A	Survival during the fire (by utilizing unburned areas) and not recolonization (from unburned areas), was the most plausible explanation of the population dynamics following fire	U (Outside perimeter)	N/A	N/A
Hylander 2011	Investigate survival of forest floor dwelling snails within harvest units, burned areas and undisturbed controls	Forest floor dwelling land snails	Southern Stockholm county, Sweden	Six to 7 samples under aspen trees in each of five burned sites and 7 forest reference sites	Scots pine and Norway spruce dominated forests with aspen trees	Selection of nearby reference (unburned) forest	Measured 2-7 years post fire	N/A	Lower abundance of snails in the burned sites as compared to the unburned reference sites	U (Outside perimeter)	N/A	N/A
Brennan et al. 2011	Determine invertebrate survival in burned plants	Invertebrates	Western Australia	Nine plants	Eucalyptus forest/ woodland	Portions of plants that did not burn	N/A	One plant	Even burned plants can provide refugia for some taxa in portions of their canopy	U/L	P	P
Banks et al. 2012	Understand animal behavior (i.e., den sharing) differences within burned areas compared to fire refugia	Mountain brushtail possum (<i>Trichosurus cunninghami</i>)	Cambarville, Victoria, south-eastern Australia	Fifty ha of burned and unburned areas	Mountain ash dominated forest	Unburned mountain ash, containing trees over 12–200 years old that contained hollows	N/A	Approximately half of a 50 ha study site	(1) Den sharing with kin was reduced in the burned area, likely because post-fire range-shifts by individuals caused kin to no longer be in close proximity (2) In unburned areas den sharing with kin increased, likely because the local population in refugia more than doubled (due to migration out of the fire) increasing competition for dens	U	S	N/A
Watson et al. 2012	Examine the avifauna at recently burned sites within extensive semi-arid shrublands of south-eastern Australia	Avifauna	Southeastern Australia	Seventy-two sites <5 years since fire and 26 sites 10 years since fire	Semi-arid shrublands	Unburned area outside of fire perimeter	Greater than 27 years	>5 ha	Species richness was higher at places close to the unburned areas <5 years after the fire, however these patterns were not evident 10 years following the fire	U (Outside perimeter)	N/A	N/A

Borchert and Borchert 2013	Compare rodent abundance and species composition in burned and unburned chaparral along fire perimeter	Four species of small mammals	Southern California, USA	Two 8×12 trap 10m grids 110 m apart	Chamise chaparral	Unburned area outside of fire perimeter artificially created by a bulldozer	Measurements up to 9 years after fire	N/A	(1) Some species did not return to the burn site 10 years after the burn, (2) some species had higher abundances in unburned areas, (3) longer-term studies are needed to capture the full dynamics of population recovery following a fire	U (Outside perimeter)	S	N/A
Radford et al. 2013	Examine whether patches of <i>Callitris intratropica</i> act as refuges for other fire-sensitive biota	Cypress Pine <i>Callitris intratropica</i> (a fire-sensitive tree)	Northwestern Australia	Surveyed several <i>Callitris</i> patches at 3 different sites	Eucalypt savannas	Patches of the fires intolerant <i>Callitris</i>	N/A	50 m to 100 m in diameter	<i>Callitris</i> patches were not found to have an abundance of fire sensitive species and might therefore not act as important fire refuges	U/L	P	P
Cullinane-Anthony et al. 2014	Examine bird diversity and uniqueness of species in fire refugia vs. burned areas	Northern Lower Michigan, USA	Seven sites ranging from 9825 ha to 65 ha	Jack pine (<i>Pinus banksiana</i>) forests	“Stringers” or “patches of residual forest” – contiguous areas of mature trees within burn perimeters	Aerial photo interpretation	N/A	N/A	Bird assemblages differed between refugia and surrounding burned landscape when burn were < 12 years old, but not when burns were >30 years old	U/L	S	N/A
Zaitsev et al. 2014	Evaluate the connectivity of (relatively) unburned litter and soil in the recovery of soil fauna communities after a fire	Soil fauna communities	Central Sweden	Three transects with 4 plots each	Sparse forest of Scots pine and common silver birch	Unburned areas, 20 m from forest edge	N/A	2–10 m ²	External colonization (of the unburned forest edge) dominates over the local survival and recovery from small refuges nearby	U/L	S	N/A
Berry et al. 2015b	Assess bird responses to the spatial patterns of unburned areas in a woodland area	All observed and heard birds	Southern Australia	Five replicated blocks within a recently burned woodland area of 28,000 ha compared to 6 sites adjacent to fire	Mallee woodland area	Unburned residuals or unburned patches	Five years following fire	Study included large (5–7 ha) and small (1–3 ha) unburned areas	Large rather than small unburned areas are needed to conserve avian diversity in fire-prone landscapes	U	S	N/A
Swan et al. 2016	Investigate how two small mammal species used unburned gully systems after prescribed fire	Bush rat <i>Rattus fuscipes</i> , agile antechinus <i>Antechinus agilis</i>	Victoria, Australia	400 ha prescribed burn area, 300 ha control	Eucalypt forest	Unburned gullies within a prescribed burned matrix	Measured twice post-fire within 1 year of burn	52% of treated area was unburned (208 ha)	<i>Agile antechinus</i> abundance increased in gullies post-fire; fire effects has little impact on bush rat abundance in refugia	U	P	P
Adie et al. 2017	Compare richness, composition and functional traits of refugia to contiguous forest	Tree species	Drakensberg mountains, South Africa	Census of woody plants in refugia, 25x10 m random plots in forests	Afromperate forests	Small patches of forest surrounded by grassland matrix	N/A	10 – 100s m ²	Richness, composition, and functional traits were indistinguishable between refugia and forests	U/L	P	P
Barbé et al. 2017	Investigate the role of residual boreal forest patches as refugia for bryophytes and compare to undisturbed forest	192 bryophyte taxa	Western Quebec	303 5x10 m plots (117 in undisturbed, 108 in residual patches, 78 in burned matrix)	Black spuce boreal forest	Areas of surviving overstory forest	Measurements 8 to 42 years post-fire	0.05 – 1820 ha	Residual patches house bryophyte species absent in burned matrix, but do not conserve all diversity present in undisturbed forest	U/L	S	E

Lutz et al. 2017	Investigate the role of pre-fire shrub cover to post-fire burned and unburned shrubs	16 species of riparian, generalist, and montane shrubs	Central Sierra Nevada	1204 shrub patches $\geq 2 \text{ m}^2$ within a 25.6 ha spatially explicit forest plot	Sierra Nevada mixed-conifer forest	Areas of unburned shrub cover	N/A	N/A	Unburned shrub patches persist on the landscape at a density and abundance potentially important for post-fire regeneration	U/L	P/S	N/A
Landesmann and Morales 2018	Characterize post-fire seedling establishment of a fire-sensitive conifer species as a function of refugial seed source and site characteristics	Cordilleran Cypress (<i>Austrocedrus chilensis</i>)	Northwestern Patagonia, Argentina	7 residual stands of <i>Austrocedrus chilensis</i> within recent large fire perimeters	Fire-sensitive conifer (<i>Austrocedrus chilensis</i>) forest	Remnant stands of <i>Austrocedrus chilensis</i> that survived fire	3 sites sampled 14 years post-fire, 4 sites sampled 17 years post-fire	N/A	Fire refugia and the surviving seed sources they contain are critical for the post-fire reestablishment of a fire sensitive conifer species	U/L	P	P

^a Burn severity; studies that include only unburned (U) or also low severity fires (L) into their fire refugia definition. ^b Predictability; studies that mainly investigate or describe predictable (P) or stochastic (S) fire refugia. ^c Persistence; studies that mainly investigate or describe persistent (P) or ephemeral (E) fire refugia. N/A indicates that there was no clear indication of the studied refugia belonging to a given fire refugia taxonomy class.

WebTable 2. Summary of reviewed studies involving landscape-scale wildfire refugia.

Study	Objective of study	Location	Extent / spatial domain of study	Ecosystem type	Fire refugia definition or characteristics	Method for spatial characterization of refugia	Refugia age	Refugia size	Main conclusions	Severity ^a	Predictability ^b	Persistence ^c
Eberhart and Woodard 1987	Assess number and size of unburned islands within fire perimeters	Alberta, Canada	Alberta north of 54N; about 400,000 km ²	Boreal forest	An unburned patch as determined from aerial photos	Aerial photography, supplemented by field data	N/A	Ave: 2–9 ha, except for fires less than 40 ha (where there were zero)	There are unburned patches in fires of all sizes (size increasing with fire size), but the unburned patch size is not always big enough for taxa of interest (i.e., elk herds)	U/L	P	E
Camp et al. 1997	Identify occurrence and attributes of late-successional wildfire refugia	Swauk Late Successional Reserve, Washington, USA	487 plots across 47,000 ha, ~12% late successional forest	Dry forests of the Inland West	(1) different (forest) structure from surrounding matrix, (2) different fire regime from surrounding matrix, (3) presence of old individuals of fire-intolerant tree species	(1) Plots, (2) GIS (characterized potential late successional forest)	130–150 years	Range: <10– 41 ha	Different combinations of topographic characteristics best predicted refugial presence	U/L	P	P
Kushla and Ripple 1997	Investigate the role of terrain variables on fire-related forest mortality	Willamette National Forest, Oregon, USA	Sample points (23, 31, 71 and 71) within 4 physiographic areas within a 3,669 ha burned area	Conifer dominated, moist, temperate forests	Refugia not used; but live canopy ratios could be interpreted as refugia indicating high survival of trees during the fire	Aerial photo interpretation	N/A	N/A	Topography and vegetation variables were significant predictors of live canopy ratio, but the specific predictors that were important varied between four physiographic areas within the burned area	U/L	P	N/A
Turner et al. 1999	Quantify (1) pre-fire heterogeneity effects of the landscape on fire severity (2) post-fire patterns of burn severities on plant reestablishment	Yellowstone, Wyoming, USA	Three sites (100 sampling points within 3 1×1-km grids)	Subalpine Forests	Unburned areas: no sign of fire effects, Light surface burn: low-intensity surface fire in which canopy trees retain green needles	Aerial observation, field observations (plots) for burn severity situation within grid	Measured up to 4 years after fire	Total: 9.7 ha (unburned); 31.3 ha (unburned+ slightly burned) of 1×1 km grid	(1) In lightly burned areas, percent cover returned to unburned levels within 3 years, (2) biotic cover tended to be higher near unburned or lightly burned areas	U/L	N/A	N/A
DeLong and Kessler 2000	Compare fire refugia forest structure to the surrounding high-severity burned landscape matrix	British Columbia, Canada	About 660,000 ha	Sub-boreal spruce forest	A remnant forest patch is older forest surrounded by younger (previously burned) forest	Maps of stand age	Assessed as a chronosequence based on persistence of different fire refugia	<10 ha	Remnant patches were different from the surrounding, younger matrix, remnant patches were also different from matrix of same age class	U/L	N/A	N/A

Clarke 2002	Compare vegetative species composition and fire response traits on habitat islands (created by topography) and surrounding open forest matrix	Four coastal and sub-coastal locations in Australia	Approximately 32 paired 0.1 ha samples of rocky outcrops versus forest matrix	Open Eucalypt forest	Fire shadows are areas that receive less fire than the surrounding matrix (mainly due to topographical effects and fuel discontinuity)	Aerial photography	Outcrops have fire return interval different from forest matrix	Size >0.1 ha (mainly for sampling purposes)	(1) Fire effects less on outcrops than in the forest matrix because the physical barrier of rock edges, (2) more frequent fires lead to less obligate seeders in the forest matrix, (3) in contrast, there is convergence towards resprouters in the forest matrix	U/L	P	P
Wimberly and Kennedy 2008	Model the sensitivity of fire spread in relation to (1) different successional stages, and (2) the distribution of fire refugia	Experimental model runs in landscapes in the interior Pacific Northwest, USA	Grids of 200×200 cells (cell size undefined)	Dry forests of the interior Pacific Northwest	Refugia in the model were defined as a land types with a lower probability of fire spread	Prescribed in modeling exercise	Old closed-canopy forests <10% of the landscape after 100,000 simulations years	Prescribed at 25–50% of landscape (in 32×32 or 64×64 squares)	The area of old closed-canopy forests increased when fire spread was less rapid in these forests, and when the physical landscape incorporated more fire refugia	U/L	S	P
Weisberg et al. 2008	Compare old-growth distributions with spatial models of fire risk to determine if old-growth pinyon-juniper woodlands are limited to sites with lower fire risk	Shoshone Mountain Range, central Nevada, USA	Nineteen-km ² watershed, age classes of stand were mapped over a 10-km ² area	Piñon-juniper woodlands in central Great Basin	Old-growth pinyon-juniper woodlands	Aerial photo interpretation and field-based adjustments to GIS layers	800-1350 years (based on old growth ages)	Ave: 9.32 ha	Old-growth piñon-juniper woodlands occupy isolated sites with low fire risk; statistical relationships between old growth and fire risk were weak implying that woodland expansion may be driven by other factors than fire exclusion	U/L	P	P
Burton et al. 2008	Examine how large fires generate landscape heterogeneity in the North American boreal forest	All boreal ecozones in Canada	All large fires across Canada from 1959 to 1999	Boreal ecosystems	Unburned islands as determined by dNBR from satellite data. Severity thresholds established based on field data (CBI)	Landsat	N/A	Ave: 14.5 ha (range: 1.3–24.2 ha; of 5 fires)	The occurrence of unburned islands was related to more unburned area within the perimeters of larger fires	U	N/A	N/A
Roman-Cuesta et al. 2009	Evaluate the importance of biotic/abiotic variables influencing the number and size of unburned islands	The Solsones wildfire, northeastern Spain	One 3,400 ha wildfire	Mixed conifer and oak	Satellite-derived land cover classes including unburned vegetation	Satellite derived fire severity map (three classes) using the Indian satellite IRS LISSIII	N/A	Ave: 0.42 (+/- 0.05 se) ha (range: <0.5–135 ha)	Unburned islands occur at continuous slopes with more forest cover and lower percentage broadleaf species	U/L	N/A	N/A
Kolden et al. 2012	Characterize abundance, distribution, and shape of unburned patches with respect to fire size and severity	Yosemite, Glacier and Yukon-Charley National Parks, USA	Yosemite: 4,771 km ² Glacier: 29,850 km ² Yukon-Charley: 30,980 km ²	Yosemite: mixed conifer shrubland Glacier: subalpine and submontane; Yukon-Charley: boreal forest	Either a 0.09 ha or a 0.81 ha area with a dNBR not detectable as burned	Classification from Landsat-derived dNBR, unburned patches were classified using thresholds (-100 ≤ dNBR ≤ 100)	N/A	Yosemite: ave. ~4 ha (range: 0.09–300 ha) Glacier and Yukon-Charley: ave. ~1 ha (range: 0.09–20 ha)	Unburned proportion significant in all areas but amount, spatial pattern, and distance within the fire to unburned varies among regions	U/L	N/A	N/A

Mackey et al. 2012	Identifying ecosystem 'greenspots' that may have functioned as habitat refuges	Great Eastern Ranges, New South Wales, Australia	24 million ha	Coastal forests, heathland, rainforests, alpine herbfields, and semiarid woodlands	Greenspots are defined as locations that may have functioned as drought and fire micro-refuges for multiple species	Satellite imagery (MODIS)	Minimally disturbed pixels from 10 year time series	Greenspots were 0.2% of total study area (Range: 86–15,238 ha)	Ecosystem greenspot index can be used to map locations that may have functioned as micro-refuges from drought and fire for a decade following the year 2000	N/A	P	P
Collins et al. 2012	Assess the effect of fire frequency on forest structure	Eastern Australia	Not explicitly stated, but about 250 km ²	Eucalyptus forest	Sites burnt two or fewer times over 27 years or >18 years between the two most recent fires	Digitized fire history layers	N/A	20×20m quadrats, size not explicitly delineated	Gullies or areas of markedly different topography in a landscape allow persistence of complex structure (generally, fire burns less severely and consumption is lower)	U/L	P	P
Kashian et al. 2012	Describe the natural range of variability in fire refugia spatial pattern	Northern Lower Michigan, USA	Not explicitly state but about 300 km ² . 54 wildfires > 80 ha examined and 11 had refugia.	Jack pine (<i>Pinus banksiana</i>) forests	“Stringers” or “patches of residual forest” where contiguous areas of mature trees within burn perimeters	Aerial photo interpretation	N/A	Mean patch area within each fire ranged from 0.1 ha – 22.9 ha	All stringers were long and narrow in size, and made up 3%-14% of burned landscapes. Fires < 80 ha did not have refugia, but larger fires had a lower proportion of their landscape as refugia, but refugia patches were larger. Neither pre-fire species composition nor topography were related to refugia creation	U/L	N/A	N/A
Andison and McCleary 2014	Quantify (1) historical range of burn severity and (2) differences in fine-scale burn patterns across ecological zones	Western boreal Canada	Wildfires across more than 100 million ha of western boreal Canada	Five Canadian boreal ecozones	Undisturbed island remnants: Unburned or partially burned areas within fire perimeter not connected to the outer unburned edge, Matrix remnants: unburned areas connected to the outer unburned edge	Aerial photo interpretation	N/A	12% (undisturbed remnants) 41% (partially burned) (range: >0 – 58% area of undisturbed remnants)	The southwestern parts (2 ecoregions) had less area in partially disturbed island remnants relative other areas, but most metrics were ecozone invariant	U/L	N/A	N/A
Leonard et al. 2014	Characterize unburned patches within a large wildfire and identify contributing factors	Victoria, Australia	250,000 ha	Eucalypt forest	Unburned as delineated from 15cm aerial imagery	Aerial imagery and SPOT-derived dNBR	N/A	Ave: 27.1 ha (range: 1-306 ha)	Unburned area was <1% of fire and mostly topography-driven	U	P	P
Perera and Buse 2014	Synthesize literature, create awareness, and explore future knowledge requirements of wildfire residuals in boreal forests	The boreal biome in the northern hemisphere	Approximately 12×10 ⁶ km ²	Boreal forests	All vegetation structure remaining following a fire	Synthesis of scientific literature	N/A	N/A	0.5×10 ⁶ ha of residual patches are produced every year across the boreal biome; growing recognition of the importance of boreal wildfire residuals will prompt answering many questions on their ecology	N/A	N/A	N/A

Kolden et al. 2015	Correlate unburned islands to climate predictor variables	Yosemite, Glacier and Yukon-Charley National Parks, USA	Yosemite: 4,771 km ² Glacier: 29,850 km ² Yukon-Charley: 30,980 km ²	Yosemite: mixed conifer shrubland Glacier: subalpine and submontane; Yukon-Charley: boreal forest	Persistent patches which have no significant spectral change between pre- and post-fire Landsat-derived dNBR;	Classification from Landsat-derived dNBR	N/A	Same as Kolden et al. 2012	No trend in unburned proportion over time and relationships between unburned islands and climate echo broader fire-climate relationships	U/L	N/A	N/A
Berry et al. 2015a	(1) Validate predictive fire refugia model using burn severity from a large, recent wildfire (2) examine the extent to which local fire severity was influenced by the severity of the surrounding landscape	Victoria Central Highlands, northeast of Melbourne, Australia	Not explicitly given, based on maps, each of the 2 catchments were roughly 12 by 12 km	Australian wet montane forest	Unburned or lightly burned habitat patches within the boundaries of a large fire	Normalized Burn Ratio from SPOT satellite imagery	N/A	N/A	Modeled fire refuges were strong predictors of fire severity, but under extreme fire conditions fire refuges were limited to areas with extremely high probability of refuge occurrence: deep, extremely sheltered mesic gullies and late successional vegetation communities; under moderate conditions fire severity was topographically mediated	U/L	P	P
Landesmann et al. 2015	Contribute to understanding of the ecological functioning of fire refuges, i.e., examine buffering capacity for fire-sensitive tree species which inhabit fire-prone landscapes	Nahuel Huapi National Park, northwestern Patagonia, Argentina	Thirty-one forest remnants throughout the national park: 24 within the area burned more than 100 years ago and 7 in the area burned less than 20 years ago	Fire-sensitive conifer (<i>Austrocedrus chilensis</i>) forest	Fixed locations where physical conditions decrease fire severity, allowing the persistence of fire-sensitive forest taxa or communities	Distribution map of <i>A. chilensis</i> forest	>100 years	N/A	<i>A. chilensis</i> forest remnants in northwestern Patagonia are persistent entities, i.e., fire refuges associated with particular biophysical attributes	U/L	P	P
Krawchuk et al. 2016	Determine predictability of fire refugia location across topographic and weather gradients	Western Canada	Seven study fires in conifer-dominated forest of the Western Cordillera of Canada	Conifer forest	Unburned or low-severity burned areas fires (-200 ≤ dNBR ≤ 200)	Normalized Burn Ratio from Landsat TM and ETM imagery	N/A	N/A	The predictability of refugia was lowest under higher fire weather conditions and increased with topographic complexity. Topographic predictors associated with refugia changed in importance with fire weather and topographic complexity	U/L	P	P
Wilkin et al. 2016	Compare fire occurrence, frequency and severity within cold air pools to the surrounding landscape matrix	Yosemite National Park, USA	Mixed conifer forests of Yosemite National Park between 1000 and 3600 m	Mixed conifer forest and scattered meadows and shrublands	Unchanged areas as determined by RdNBR fire severity maps	Relative differenced Normalized Burn Ratio (RdNBR) from satellite data	N/A	N/A	The landscape scale study suggests that cold-air pools have lower fire occurrence, frequency, and severity patterns, possibly leading small-scale refugia	U/L	P	P
Ouarmim et al. 2016	Test if particular environmental conditions and stand characteristics explain the presence of fire refugia	Northwest Quebec, Canada	11,000 ha natural forest mosaic	Boreal mixedwood forest	Late-successional conifer stands which escaped two of more consecutive fires	Stand composition maps, dendrochronological and palaeoecological fire histories	> 250 years	N/A	Fuel moisture is the dominant factor influencing the distribution of fire refugia, which are assumed to not be randomly distributed	U/L	L	P

Meddens et al. 2016	Develop a model for classifying unburned areas within wildfire perimeters using moderate resolution satellite and ancillary data	Interior Pacific Northwest, USA	Twenty fires and 868 field plots	Forests and rangelands of the Inland Northwest	Unburned plot locations evaluated by field visits	Multi-temporal Landsat and ancillary data	N/A	Ave unburned by fire: 19% (standard deviation 16%)	(1) Using multi-date Landsat scenes improved classification accuracy of unburned areas, (2) the total area of unburned islands in non-forest was significantly higher than the unburned areas in forest	U	N/A	N/A
Nielsen et al. 2016	Assess influence of lake pattern on fire frequency and the predictability of fire refugia	Boreal Shield and Boreal Plain, northern Saskatchewan Canada	All large fires (>200 ha) between 1980 and 2014	Boreal forest	Parts of the landscape where intense crown fires are rare	Mapped fire perimeters from Canadian Forest Service National Fire Database	N/A	N/A	Persistent landscape features can reduce the likelihood of wildfire. Areas close to lakes are more likely to lead to long-term fire refugia	U	P	P
Haire et al. 2017	Quantify neighborhood spatial patterns of refugia and characterize plant species composition along a neighborhood gradient	Jemez Mountains, New Mexico, USA	Las Conchas fire (2011, 61,000 ha)	Mixed conifer forest	Areas which have no significant spectral change between pre- and post-fire Landsat-derived dNBR; ($-200 \leq \text{dNBR} \leq 200$)	Classification from Landsat-derived dNBR	N/A	N/A	Neighborhood patterns were correlated with topographic predictors. Most refugial neighborhoods overlap with refugia from previous fires	U/L	P	P
Banks et al. 2017	Simulation experiment to investigate how fire regimes interact with topography and weather to shape genetic diversity	Australian Alps, Australia	9,125 km ²	Montane forests	Upper 20 th percentile of mean interfere interval	Simulation	N/A	N/A	Topographic relief and weather variability influence occurrence of refugia. Refugia patterns have implications for genetic diversity and spatial structure	U/L	P	P
Kolden et al. 2017	Sustainability of previously classified wildfire refugia following a contemporary fire event	Swauk Late Successional Reserve, Washington, USA	Plots (122) across 3 drainages, approximately 11 ha in total	Dry forests of Inland Northwest	Does not transition between successional stage due to fire	Field data and supplemental information	Same as Camp et al. 1997	Same as Camp et al. 1997	(1) Extreme fires can maintain historic range of variability of successional stages across landscape, (2) historic refugia burned more severely in 2012 than surrounding forest, (3) new refugia formed, suggesting refugia are ephemeral or "shift" over time	U/L	S	E
Meddens et al. 2018	Determine unburned proportion trends across the Northwestern US from 1984–2014 and assess patterns across space	Interior Pacific Northwest, USA	Entire interior Pacific Northwest, USA	Forests and rangelands of the Inland Northwest	Unburned plot locations as determined by Meddens et al. 2016	Multi-temporal Landsat data	N/A	Ave. unburned patch size is 1.2 ha (sd: 25.4 ha) Ave. unburned proportion by fire: 9.6%,	Unburned area proportion exhibited no change over the three decades; ecoregional differences in mean unburned proportion, patch area, and patch density, suggests influences of vegetation and topography on the formation of unburned areas	U	N/A	2.6% of total unburned area was unburned for >2 fires

Rogean et al. 2018	Investigate the influence of topographic features on fire refugia persistence	Alberta Rockies, CA	911,951 ha	Forest capable landscapes in the Alberta Rockies	Stands >300 years old	Field-based fire history data	>300 years	N/A	Topographic features were strong predictors of persistent fire refugia; sustainability of fire refugia may be decreasing with warming climate and current fuel conditions	U/L	P	P
Meigs and Krawchuk 2018	Characterize abundance, structure, and composition of fire refugia in the Pacific Northwest, USA	Oregon and Washington, USA	612,629 ha	Forest and non-forest area in Oregon and Washington	0 – 10% basal area mortality according to fire severity inferred from Landsat imagery	Classification from Landsat-derived RdNBR	N/A	N/A	(1) Ecological role of fire refugia depends on site-specific pre-fire conditions, as well as the broader burn severity mosaic, (2) non-forest vegetation accounted for a substantial component of fire refugia	U/L	N/A	N/A

^a Burn severity; studies that include only unburned (U) or also low severity fires (L) into their fire refugia definition. ^b Predictability; studies that mainly investigate or describe predictable (P) or stochastic (S) fire refugia. ^c Persistence; studies that mainly investigate or describe persistent (P) or ephemeral (E) fire refugia. N/A indicates that there was no clear indication of the studied refugia belonging to a given fire refugia taxonomy class.

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